REPORT DOCUMENTATION PAGE			Form Approved OMB No. 0704-0188
Public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information including suggestions for reducing the burden, to Department of Defense, Washington Headquarters Services, Directorate for Information Operations and Reports (0704-0188), 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to any penalty for failing to comply with a collection of information if it does not display a currentity valid OMB control number. PLEASE DO NOT RETURN YOUR FORM TO THE ABOVE ADDRESS.			
1. REPORT DATE (<i>DD-MM-YYYY</i>) 17-12-2008	2. REPORT TYPE Final Report		3. DATES COVERED (From – To) 8 September 2005 - 08-Nov-08
4. TITLE AND SUBTITLE Multisensory mechanisms of gaze stabilization and flight control		5a. CONTRACT NUMBER FA8655-05-1-3066 5b. GRANT NUMBER	
		SD. GRANT NOMBER	
		5c. PROGRAM ELEMENT NUMBER	
6. AUTHOR(S) Dr. Holger G Krapp		5d. PROJECT NUMBER	
gg. 0		5d. TASK NUMBER	
		5e. WORK UNIT NUMBER	
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Imperial College London South Kensington Campus London SW7 2AZ United Kingdom			8. PERFORMING ORGANIZATION REPORT NUMBER N/A
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) EOARD Unit 4515 BOX 14 APO AE 09421			10. SPONSOR/MONITOR'S ACRONYM(S) 11. SPONSOR/MONITOR'S REPORT NUMBER(S) Grant 05-3066
12. DISTRIBUTION/AVAILABILITY STATEMENT			
Approved for public release; distribution is unlimited.			
13. SUPPLEMENTARY NOTES			
This report results from a contract tasking Imperial College London as follows: The grantee will investigate the sensory mechanisms of gaze stabilization and flight control on insects (flies and locusts). The study aims at understanding the underlying biological design principles. The research includes techniques ranging from neurophysiology and neuroanatomy to quantitative behavioral observations complemented by analytical and numerical modeling. Focus is on multi-sensory integration (visual and mechanosensory information), biophysical mechanisms of looming detection (visual information), and the use of efference copy for sensory information processing as well as inner and outer loop control. In summary, we find that the rotations associated with the lateral modes of motion we have identified in <i>Calliphora</i> are orthogonal to the axes of maximal sensitivity of the VS interneurons, but approximately coincide with the axes of maximal sensitivity of the HS interneurons. None of the identified LPTCs in flies appear to be tuned to sense forward translation, but we have found that locusts do monitor several axes of translation – including straight flight, which is the primary flight mode of this species (c.f. flies). These results are consistent with the original hypothesis which we set out to test: that visual interneurons processing self-motion information are tuned to the preferred modes of flight behaviour of the insect in question.			

17. LIMITATION OF ABSTRACT

UL

18, NUMBER OF PAGES

15. SUBJECT TERMS

a. REPORT

UNCLAS

EOARD, Flight Control, Biology

b. ABSTRACT

UNCLAS

c. THIS PAGE

UNCLAS

16. SECURITY CLASSIFICATION OF:

19a. NAME OF RESPONSIBLE PERSON

19b. TELEPHONE NUMBER (Include area code)

TAMMY SAVOIE, Lt Col, USAF

+44 (0)1895 616459

Department of Bioengineering Imperial College South Kensington Campus London SW7 2AZ email: h.g.krapp@imperial.ac.uk

"Multisensory Mechanisms of Gaze Stabilization and Flight Control"

(Period of finding: October 2005 – September 2008)

Final report

Contents:

- 1. General Summary of Achievements
 - 1.1 Publications
 - 1.2 WOS Projects
 - 1.3 Funding
 - 1.4 Visibility
 - 1.5 Group Size, Collaborations, and Scientific Impact
- 2. Report on Current Projects
 - 2.1 Sensory and Motor Control Axes
 - 2.2 Neck Motor Neurons
 - 2.3 Multimodal Activity Modulation of LPTCs
 - 2.4 Sensory Processing, Multisensory Integration, and Efference Copies in Behaving Animals
 - 2.5 State-dependent Processing in LPTCs
 - 2.6 Characterization of Head Movements in the Blowfly
 - 2.7 Visual Distance Control
- 3. Concluding Remarks
- 4. Additional References
- 5. PI Reference List

1. General Summary of Achievements.

The purpose of the grant FA8655-05-1-3066, "Multisensory Mechanisms of Gaze Stabilization and Flight Control", was to generally support research in my lab rather than to fund a specific project. At the time the grant was awarded it was the necessary condition for me being eligible to submit a research proposal to the BBSRC (Biotechnology and Biological Sciences Research Council, UK) and to investigate, together with Prof Simon Laughlin and Dr Graham Taylor (see below) the relationship between visual sensor axes and flight modes in locusts and flies. Soon after the BBSRC grant was awarded I commenced a permanent position in the Department of Bioengineering, Imperial College, UK, which allowed me to use the USAF Research Laboratory funding to employ an additional Research Assistant (RA = postdoc) in my lab.

The last three years during which my lab was funded by the USAF Research Laboratories have been extraordinarily productive. Despite the fact that (a) my lab

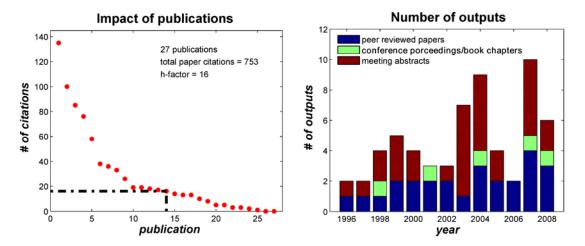
had to move twice - from Cambridge to temporary space at Imperial College London and then to our new, dedicated rooms – and (b) that I was appointed Director of Postgraduate Studies (Research) being responsible for about 70 PhD students in the Department of Bioengineering, the overall progress, achievements and visibility were highly competitive at the international level. This is reflected by a couple of performance parameters including publications (1.1), WOS Projects (1.2), Funding (1.3), Visibility (1.4), and Group size as well as international collaborations (1.5).

In this final report I will concentrate on the performance parameters and will give a brief summary of the scientific progress which, to a great extent, is covered by my previous report submitted in July 2008. I should emphasise that, although I have been receiving funding from various sources, the support from the USAF Research Laboratory was the main driving force in the progress my group has made within the last three years.

1.1 Publications

During the supported period, together with my collaborators, I have published 11 peer reviewed papers, some in high profile Journals such as PLoS Biology, Current Biology, and Journal of Neuroscience, one comprehensive book chapter on central visual processing in insects, one conference proceeding, and 11 meeting abstracts.

Bibliographic Parameters



Additional abstract citations = 28. Data based on Google Scholar. Snapshot on 7. December 2008

For more specific information, please see my personal reference list at the end of this report.

1.2 WOS projects

From 2003, i.e. two years before the funding started, until 2008, I have applied for and was awarded *6 WOS grants*. These projects have been, without exception, extremely helpful and inspirational (see my WOS reports). They funded the presentation of my work at the 1st and 2nd workshop on compound eyes, University of

Arizona, Tucson, two invited talks at the annual meeting of the Institute of Navigation, and two visits to the AF Research Laboratory in Eglin, FL. The last visit to the Res Lab at Eglin Air Force Base end of April 2008 was particularly exciting. On-base briefings on two days gave me the opportunity to meet some of the contractors working in areas close to my field of expertise. At one of the meetings I met Dr Sean Humbert, with whom I currently apply for a USAF Res Lab (AFOSR) project grant (see below). Another outcome of my last WOS visits to Eglin AFB was that it would be highly desirable to institutionalize my annual visits to the Research Laboratory.

1.3 Funding

During the funded period I have written and submitted a number of grant proposals, some of which were successful, some were revised and resubmitted and some will be rewritten and sent to alternative funding agencies. The funding secured over the last 3 years is in excess of £1M and includes a grant from the prestigious HFSP (Human Frontier Science Project) trust.

Funding secured for research in my laboratory (excluding FA8655-05-1-3066):

- **BBSRC** research collaboration PI, with Prof Simon B. Laughlin, Co-PI University of Cambridge, UK, and Dr Graham Taylor, PI Oxford University, UK: "Tuning of the preferred optic flow axes of locust and blowfly visual interneurons to their preferred modes of flight behaviour."
- **HFSP** research collaboration PI, with three other PIs: Drs. Manos Drakakis, Imperial College, Fabrizio Gabbiani, Baylor College of Medicine, TX, USA, Martin Egelhaaf, Bielefeld University, Germany: "Comparative analysis of RF-transmitted neural activity on flying insects."
- Air Force Research Laboratory/EOARD, PI: "Multisensory Control of Stabilization Reflexes."
- Air Force Research Laboratory/EOARD, Co-PI, with Prof Simon B. Laughlin, PI University of Cambridge, UK: "Multisensory Integration in Fly Lobula Plate Tangential Cells."

Funding secured for Department of Bioengineering (PhD programme):

• BBSRC Doctoral Training Grant.

Grant proposals under consideration:

- **AFOSR/NL**, through EOARD, PI, together with Dr Sean Humbert, PI University of Maryland: "The relationship between visual sensor equipment in flying insects and their flight performance a 'Neurobio-Engineering' approach".
- **EPSRC** (Engineering and Physical Sciences Research Council, UK) research collaboration, PI together with three other PIs, Drs. Anil Bharath, Piere Luigi Dragoti, Manos Drakakis, Imperial College, UK: "Biologically inspired motion processing on VLSI devices."

Grant proposals in preparation:

- BBSRC, PI, named RA Dr. Martina Wicklein. This grant proposal on "Neuronal Basis Underlying Visual distance control" was turned down but will be revised and resubmitted to the BBSRC. We propose a kinematic, dynamic and neurophysiological analysis of the hovering behaviour in hawkmoths.
- Framework Programme 7, European Research Council, research collaboration, PI, together with Professor Alessandro Astolfi, Dept. EEE, Imperial College London, Professor Patrizio Colaneri, PI, Dept. of Electronics and Information, University of Milano, Italy, Dr Fritz Lehmann, PI, Neurobiology, University of Ulm, Germany. This international research collaboration is in its preproposal stage. Building up on previous research on the "Berkeley Fly" we propose to work on "Bio-inspired Control of Micromechanical Insects" by integrating the expertise of scientists working on biological sensing and control, insect aerodynamics, and control engineering. This research collaboration in combination with the proposal submitted to AFOSR/NL should yield a synergetic effect on the development of MAVs.
- EPSRC, PI, together with Dr. Manos Drakakis, Dept Bioengineering, Imperial College, on the development of bio-inspired VLSI sensors for optic flow processing. The goal is a generic optic flow sensor that can be implemented in a wide range of applications.

1.4 Visibility

Invited talks: from 2005 to 2008 I have been invited to give *11 seminar talks* as well as *9 presentations at international conferences/workshops* (cf. CV for details).

Media coverage: Imperial College 'News and Events' interview/video-interview 2008, London Times interview 2008, Imperial College press release on latest publication in PLoS Biology 2008, Reporter (Imperial College) 2008, Interview "Die Zeit", Germany, 2008

1.5 Group size, Collaborations, and Scientific Impact

Group size: Between early 2005 (Cambridge) and end 2008 (Imperial College) my group size has increased from 2 postgraduate students to currently 2 RA and 3 postgraduate students. In addition each year I supervise at least one summer student as well as 1-2 final year undergrad or MSc projects.

Collaborations: Within the UK I currently collaborate with groups in Cambridge, Oxford and groups at Imperial College. International Collaborations include currently the University of Bielefeld, Germany, Baylor College of Medicine, USA, and the USAF Research Laboratory, Eglin, US). Depending on the outcome of my recent grant applications further collaborations with the University of Maryland, US, the

University of Ulm, Germany, and the University of Milano, Italy, will be added (cf. 1.3).

Scientific Impact: Besides the publication-related impact (cf. 1.1), I regularly review scientific manuscript for 19 different Journals including Nature, PLoS Biology, and Current Biology. I am also acting as a referee for national and international grant agencies (cf. CV). Finally, I was invited by the European and National Science Foundations to assist in defining the grand challenges of future interdisciplinary research collaborations between European and US Biologists and Engineers (cf. CV.)

I was recently invited to give a presentation at a workshop organized by the Gatsby Unit for Computational Neuroscience, University College London, where I outlined the research in my lab. This international "invitation only" workshop on "Simpler Cognitive Systems" resulted in plenty of positive feedback on my presentation as well as an invitation by the editor of the Journal "Current Biology" to write about ocellar systems. Furthermore, our project on state-dependent processing using octopamine agonists (see below) was also very well received.

2. Report on current projects:

In the following I will mainly focus the latest development of the key projects (2.1-2.5). More detailed information about background and relevance of the projects can be found in my previous report (July 2008). Finally, I will describe two further projects (2.6, 2.7), which have been or will be started shortly.

2.1) BBSRC research grant collaboration: Sensory and Motor Control Axes

together with Dr Graham Taylor, Department of Zoology, Oxford University.

Project started in July 2005 – ended in September 2008

Research Associate: Dr Daniel Wüstenberg.

PI: Holger G Krapp (HGK), Department of Bioengineering, Imperial College London Co-PI: Simon B Laughlin, Department of Zoology, University of Cambridge

This project was based on the hypothesis that the sensor axes along which flying insects measure self-motion parameters are aligned with those motor axes the animals use to control their specific (aerodynamic) modes of flight (O24). To test the "mode-sensing" hypothesis, we combined quantitative behavioural data (Oxford team) with the preferred rotation axes of optic flow-processing interneurons in flies and locusts obtained from electrophysiological experiments (A31).

I will attach here the final overall report on this BBSRC project which provides a summary of our achievements and will only briefly describe the electrophysiological results obtained in my lab at Imperial College.

Major electrophysiological finding: Recordings from directional-selective cells in the locust lobula were significantly more difficult to achieve than those from lobula plate tangential cells (LPTCs) known to measure optic flow parameters (O6, O24, R3). We nevertheless succeeded in studying a set of wide field neurons in locust by means of mainly extracellular and a few intracellular recordings (A31). Locusts, like flies, employ directional-selective cells with extended receptive fields. The distribution of

local motion preferences in these receptive fields suggests that they are tuned to certain self-motions which indicates they play a similar role in visually controlled behaviour as the fly lobula plate tangential cells (cf. Fig. 1, attached BBSRC report). A detailed analysis of the receptive field with respect to the preferred self-motion axes in locust shows, however, that there are marked differences between the two species (cf. Fig. 4, attached BBSRC report): (i) While flies employ a comparatively large number of LPTCs, 10 VS cells, to sense horizontal body rotations, locusts – in terms of rotations - mostly analyse turns around slightly tilted vertical body axes. (ii) Flies do not have LPTCs which cover forward translation directly, but locusts do.

The overall analysis of all experimental data obtained in this project has not been completed yet. At this point in time, therefore, we can not draw any firm conclusions. The experimental evidence however suggests that not only in dipteran flies but also in orthopteran locusts are directional-selective wide-field cells tuned to specific optic flow fields. This suggests a general functional principle in visuo-motor control. The differences in preferred self-motion axes analysed by the flies and locusts seem to reflect the species-specific adaptations to the animals' respective aerodynamic properties and flight modes. Locusts endowed with a higher degree of passive aerodynamic stability than flies apparently employ a smaller number of pitch- and roll-sensitive cells than the aerodynamically unstable but more manoeuvrable fly.

Although this project has come to an end I will continue the collaboration with Dr Graham Taylor's group to further investigate the functional relationship between sensors and actuators in insect flight based on quantitative behavioural data on insect aerodynamics. A scientific publication of the electrophysiological data is currently in planning.

This project is an essential building block for the collaborative grant proposal together with Dr. Sean Humbert (cf. 1.3) submitted to AFOSR/NL on a comparative study of sensors (compound eye/ocelli) and flight control in robber flies and horse flies (cf. proposal No: 09NL-002). My previous report in combination with the proposal contains further information about the relevance of this project in the context of the control of autonomous (micro) air vehicles.

2.2) Research Associate project on: Neck Motor Neurons

Funding from the Medical Research Council (MRC) to Dr. Stephen Huston and from USAF grant to HGK.

Supervisor: HGK

The experimental part of this project on the neuronal pathway involved in fly gaze stabilization has (temporarily) come to an end as Dr. Stephen Huston is now a postdoc at Caltech, USA. Stephen characterized the response properties of fly neck motor neurons, in particular their specificity to certain optic flow fields. His contribution was the first to show in detail how self-motion information provided by LPTCs is used in the well-defined neck motor system that controls compensatory head movements.

After the first part of Dr. Stephen Huston's work has now been published (O26) we are currently preparing a second publication on the non-linear interaction between

haltere and visual input at the level of the neck motor neurons. Stephen found that some neck motor neurons set up an "AND gate" that requires both visual and haltere (gyroscopic) input before the neurons generate action potentials which are a necessary condition to control neck muscle contraction (cf. last report, O28, A33). As I indicated in my previous report such gating mechanism may be an adaption to the kinematic properties of different muscle blocks controlling slow, intermediate and fast head movements. To test this hypothesis we have started another PhD project on the functional organization of the neck motor system (cf. project 2.6, below).

Background and relevance of this project are described in my previous report. Here, I would like to emphasise the importance of head movements for the analysis of optic flow and the significance of fast sensorimotor pathways in the context of flight control. Head movements are a necessary prerequisite for optic flow-based flight control as they stabilize a default orientation of the visual environment and thus simplify the extraction of self-motion information. For this to work, head movements need to cover an extended dynamic range which, in terms of sensor measurements, involves several complementary mechanisms (multisensor fusion). Compound eyes, ocelli and halteres provide information on attitude changes, but at different delays and for different sections of the overall dynamic input range. The neck motor system is a perfect model system to study several issues in control engineering: (i) dynamic range fractionation, (ii) multisensor fusion, and (iii) sensorimotor feedback/feed forward control. Furthermore, image stabilization is a fundamental issue in vision-based pattern matching (e.g. seekers).

2.3) PhD project on: Multimodal Modulation of LPTCs

Funding from the Biological and Behavioural Sciences Research Council (BBSRC) to Mr Matthew Parsons and from USOSR/NL to Prof. Simon Laughlin. Supervisors: Simon B. Laughlin, HGK (co-supervisor).

Two years ago Matthew Parsons demonstrated for the first time that the activity of an identified LPTC, the spiking V1 cell, is modulated by ocellar input (O20, A32). His PhD thesis is a milestone in the research on multisensory integration. Matthew has now passed his viva and will continue his work in Dr Simon Laughlin's lab and under my co-supervision on the integration of ocellar/compound eye signals for the next 11 months (funded by USAFOSR/NL, cf. 1.3).

In my last report I presented Matthew's data on intracellular recordings from VS cells. Matthew successfully recorded from 8 out of 10 VS cells, all of which received input from the ocelli. Because the spiking V1 cell, which he recorded from in his first sets of experiments, are known to receive input from VS1-VS3, it was to be expected that the activity in these cells could be modulated by ocellar input. It was not clear, however that all the other VS cells also received ocellar input. Matthew developed a quantitative ocellar stimulus which allowed him to mimic rotations of the fly around various horizontal body axes. Applying this stimulus during intracellular recordings he found that each VS cell has a preferred axis tuning, the shape of which is similar to that mediated by wide-field optic flow stimulation of the compound eye. Further data analysis showed that the distribution of ocellar-mediated preferred rotation axes seems to reflect the cardinal measuring axes the ocellar system used to sense the fly's changes in attitude, i.e. rotations around the roll axis and an axis intermediate between

pitch and roll. Apparently, the ocellar system also signals horizontal body rotations, but at a much coarser resolution than the compound eye. Matthew also performed pioneering behavioural experiments using a newly developed apparatus that stimulates both the compound eyes and the ocelli. His first results indicate that the faster ocelli responses advance the signals mediated by the compound eye and thus speed up the processing of attitude changes in the VS cells.

A more comprehensive description of the current findings, their functional implication, and future research can be found in the proposal on "Multisensory Integration in Fly Lobula Plate Tangential Cells" submitted by Prof Simon Laughlin to AFOSR/NL through EOARD. We are currently working on a scientific publication of Matthew's latest electrophysiological results and will set up for further behavioural and electrophysiological studies.

2.4) PhD projects on: Sensory Processing, Multisensory Integration, and Efference Copies in Behaving Animals

Funding from Department of Bioengineering, Imperial College, and the USAF to HGK (supplementary overseas student fees). PhD Students: a) Mr Naveed Ejaz, b) Mr Kris Peterson. Collaborator: Dr. Emmanuel Drakakis, Dept. Bioengineering, Imperial College London.

PI: HGK.

The ultimate goal of this project is to build a closed-loop experimental robot platform that will allow us to investigate multisensory integration in a closed-loop system. During the last 6 months the PhD students working on this project made significant progress in that they succeeded in closing the loop between neural activity and robot actuation/steering. This intermediate step along the project was necessary to show that it is actually possible to use neuronal activity, action potential, of an identified LPTC, H1, to control a robot.

The set up the students use still consists of a conventional electrophysiology rig and two high speed (200 fps) computer displays for visual stimulation. The fly is positioned in front of the displays, one positioned in the left, the other one in the right visual hemisphere at +/- 45 degrees relative to the animal's longitudinal body axis. External to the rig a robot, equipped with two high speed video cameras, is positioned on a turn table that is moved clockwise at slightly variable angular speed. The robot is surrounded by a pattern that consists of vertical strips, which, because of the movement of the turntable, induces wide-field motion that is picked up by the cameras and transmitted via thin wires to two PCs. The PCs output the pattern motion to the computer displays mentioned above. Due to the pattern motion, the spiking activity of an extracellularly recorded H1 cell is modulated to a degree that depends on pattern velocity. The recorded spikes are identified by a threshold algorithm and are converted into a continuous voltage signal that is fed back, via wireless Bluetooth transmission, to the RISC processor of the robot. During the first experiments the control algorithm was chosen so that the robot motor system compensates for the externally forced movement of the turn table.

With this simple "fly-machine interface" operating under closed loop conditions we could show that neuronal H1 signals are sufficient to perform an image stabilization

task. Our first results using the interface have the following significant implications for further research:

- a) Proof of concept: the experimental approach chosen to study multisensory integration under closed-loop conditions is realistic. In the final configuration, i.e. with the fly mounted on the robot, it will allow us to assess the contributions of various sensory systems to motor control while the fly is actually moving in space.
- b) Optimizing control algorithms in a closed-loop brain machine interface: this is a more general implication which addresses a fundamental issue of brain-machine interfaces. Because the sensory motor pathway in the fly is sufficiently well know with respect to its sensory input we can now study and optimize control algorithms which take into account some of the fundamental properties of biological sensor system such as neuronal noise, neuronal adaptation, and pattern/illumination-dependent sensor signal. The goal will be to develop control algorithms which are independent of visual stimulus parameters and thus allow for pattern-invariant feedback control.
- c) Characterization of biological sensor systems: So far the fly visual system has been studied by focussing on its coding properties which did not explicitly take into account the link to the various motor systems. Our new experimental platform allows us to characterize visual information processing within a solid control-engineering framework that takes into account the closed loop nature of a biological control system as well as its plasticity, adaptability, and the potential use of forward models (efference copy).

Early next year we will be featuring the new system internally at Imperial College before presenting it at the Göttingen Neurobiology Conference, Germany, 2009, and preparing a scientific publication - probably in one of the IEEE journals. With this project I finally bridged the gap between basic neurobiological research and control engineering. The potential applications go far beyond the analysis of the fly visuomotor pathways per se and will probably have an impact on the development of various technical and medical applications where brain-machine interfaces are required.

The layout of the silicon micro recording probe that will be implanted in the fly head capsule to pick up signals from spiking LPTCs has now been finalized and will be sent out for production early January. We expect to have the first prototype for testing in the lab by April 2009.

2.5) Research Associate project on: State-dependent Processing in LPTCs. Funding from the USAF to HGK. Research Associate: Dr Kristopher Longden. PI: HGK.

Dr Kit Longden has continued his work on state-dependent processing of optic flow using pharmacological drugs to switch the fly's brain from resting/walking to flight state (A32). The follow-up grant from the USAF Research Laboratory (FA8655-09-1-3022) has now been activated. Together with Mr Daniel Schwyn, PhD student (see below), Kit set up a fly colony which will provide a constant supply of experimental

animals for the lab. He also continues to be the integrating figure in my lab by helping to supervise various projects and taking on organizational duties.

I have been reporting about progress of his research in my last report (July 2008). Here I should confine myself to his latest achievements and new collaborations he initiated with the Bio-sensor groups in our Department.

By applying the octopamine agonist Chordimeform (CDM) – octopamine is a neurotransmitter, neuromodulator and neurohormone in insect nervous systems - Kit induces a fictive flight state in flies. Besides its impact on neural processing, octopamine also switches metabolic pathways, i.e. during walking and resting carbohydrates are metabolized for energy supply of muscles and neurons while during flight fatty acids are being used. He then studies the changes in neuronal processing compared to the processing in the same animals before treatment. His major findings are:

- a) The spontaneous activity of spiking LPTCs, V1 (roll-pitch sensor) and V2 (roll sensor), is significantly elevated after drug application. This effectively changes the set point of the LPTCs and allows the cells to exploit the negative and positive dynamic response range in a more efficient way.
- b) The response delay in both V1 and V2 is reduced.
- c) The information rate transmitted by V1 and V2 is increased.

Altogether, these changes can be interpreted as short term adaptations to the different dynamic input ranges flies encounter when walking/resting or flying, given energy constraints (Laughlin 2001). Less energy supply to the nervous system and the (leg) muscles is required during walking/resting. When airborne, however, the flight motor consumes considerably higher amounts of energy and the visual system, including the LPTCs, process information at higher bandwidth which is energetically more expensive. Because power constraints present a fundamental issue for micro air vehicles with limited payload, Kit's research on energy efficient coding is highly relevant for the development of low power, bio-inspired sensorimotor control systems (for further information on this project see my July 2008 report).

To include more experimental results and the information theoretical analysis in Kit's first publication we had to postpone manuscript submission by a few months. The changes on the manuscript are now nearly completed and we expect its submission in January 2009.

Kit also started to collaborate with the Bio-sensor groups of Drs. Danny O'Hare and Martyn Boutelle in the Department of Bioengineering at Imperial College. These groups have the instrumentation to measure octopamine concentrations in haemolymphe samples taken from the fly during different locomotor states. In collaboration with the Bio-sensor groups, we are also aiming to measure the changes of adenosine-triphosphate, a molecule that provides energy for any muscle and neuronal activity. The idea is to establish the correlation between neuronal processing and energy consumption during different locomotor states.

Building up on previous studies in the laboratories of Drs. Strausfeld and Hengstenberg (rev.: R3) and detailed electrophysiological experiments in my own lab (cf. 2.2, O26), Daniel Schwyn, a PhD student, is setting up the instrumentation for a functional characterization of the blowfly gaze stabilization system. Daniel has completed a first prototype of the LED arena he will be using for visual stimulation in behavioural experiments. He will perform both a dynamic and a kinematic analysis of head movements during visual stimulation – which will be eventually combined with electrophysiological recordings from LPTCs. He set up and tested our 6 DoF force transducers as well as a classic yaw torque meter for dynamic measurements. While experiencing technical difficulties with the 6 DoF force transducer (faulty channels), Daniel has successfully implemented the torque meter which will be also be used in collaborative and student projects.

To complement the characterization of the fly neck motor system an MSc student will perform electrical stimulations of neck muscles and neck motor neurons while monitoring head movements using high speed video cameras.

Understanding the functional organization of the neck motor system is an important prerequisite for any biologically inspired gaze stabilization systems which facilitates the use of optic flow for flight control.

2.7) BBSRC proposal: Visual Distance Control.

I reported on this proposal in my previous report (July 2008). We proposed a dynamic, kinematic and electrophysiological study of visual distance control in hovering hawkmoths. By integrating the results of this multi-level analysis we should derive a comprehensive model of a robust outer-loop collision avoidance system. Unfortunately, the proposal was unsuccessful when submitted for the first time. Because of the relevance of this project in the context of outer-loop flight control I decided to include work on hawkmoths into the HFSP collaboration which has now started. The HFSP-funded project is aiming to develop micro recording probes which include an RF module for wireless transmission of neuronal signals and therefore goes beyond the scope of the project Kris Peterson (2.4) is working on. The goal of the HFSP study will be to record neural activity in semi- or freely-flying locusts and flies.

I will also revise and resubmit the proposal on visual distance control to the BBSRC, or to other funding agencies, as soon as we will have obtained the first preliminary results. Dr Martina Wicklein will start her work in January 2009.

Concluding remarks

Over the last 3 years we have established an integrative System Neuroscience approach in my lab that hugely benefits from the interdisciplinary environment at Imperial College London. Funding from several sources - mainly from the USAF -, access to excellent students and the close proximity and collaboration with engineers and neuroscientists have had a significant impact on the progress we were able to achieve so far. Further collaborations with engineers at Imperial College, the US and

in Italy will help me to establish a true bridge between basic neuroscience research and bio-inspired control engineering.

Holger G Krapp

London, UK, 15. Dec 2008

Additional Reference:

Laughlin S.B. (2001). Energy as a constraint on the coding and processing of sensory information. *Curr. Opin. Neurobiol.* **11**: 475-480.

Publication List HGK

Diploma Thesis:

Krapp H.: Ein Verfahren zur schnellen Bestimmung der lokalen Vorzugsrichtung und Bewegungsempfindlichkeit im rezeptiven Feld von visuellen Interneuronen der Schmeißfliege *Calliphora erythrocephala*. Diplomarbeit. Eberhard-Karls-Universität Tübingen 1992.

PhD Thesis:

Krapp H.: Repräsentation von Eigenbewegungen der Schmeißfliege *Calliphora erythrocephala* in VS-Neuronen des dritten visuellen Neuropils. Dissertation, Eberhard-Karls-Universität, Tübingen, 1995.

Publications in refereed journals:

- O1. **Krapp H.G.** and Hengstenberg R: Estimation of self-motion by optic flow processing in single visual interneurons. *Nature*, **384**: 463-466, (1996)
- O2. **Krapp H.G.** and Hengstenberg R: A fast stimulus procedure for determining local receptive-field properties of motion-sensitive visual interneurons. *Vision Research*, **37**: 225-234, (1997)
- O3. **Krapp H.G.**, Hengstenberg B., and Hengstenberg R.: Dendritic structure and receptive field organization of optic flow processing interneurons in the fly. *Journal of Neurophysiology*, **79**: 1902-1917, (1998)
- O4. Gabbiani F., **Krapp H.G.**, and Laurent G.: Computation of object approach by a wide-field, motion- sensitive neuron. *Journal of Neuroscience*, **19**: 1122-1141, (1999)
- O5. Gabbiani F, Laurent G, Hatsopoulos N, and **Krapp H.G.**: The many ways of building collision-sensitive neurons. *TINS*: **22**, 437-438, (1999)
- O6. **Krapp H.G.** Neuronal matched filters for optic flow processing in flying insects. *International Review of Neurobiology*, **44**: 93-120, (2000).
- O7. Franz M.O. and **Krapp H.G.**: Wide-field, motion-sensitive neurons and optimal matched filters for optic flow. *Biological Cybernetics*, **83**: 185-197, (2000).

- O8. Petrowitz R., Dahmen H., Egelhaaf M., and **Krapp H.G.**: Arrangement of optical axes and the spatial resolution in the compound eye of the female blowfly. *Journal of Comparative Physiology A*: **186**: 737-746, (2000).
- O9. Karmeier K., Egelhaaf, M., and **Krapp H.G.**: Early visual experience and the receptive field organization of optic flow processing interneurons in the fly motion pathway. *Visual Neuroscience*, **18**: 1-8, (2001).
- O10. **Krapp H.G.**, Hengstenberg R., and Egelhaaf M.: Binocular input organization of optic flow processing interneurons in the fly visual system. *Journal of Neurophysiology*, **85**: 724-734, (2001).
- O11. Gabbiani F., **Krapp H.G.**, Koch C., and Laurent G.: Multiplicative computation in a looming sensitive neuron. *Nature*, **420**: 320-324, (2002).
- O12. Egelhaaf M., Kern R., **Krapp H.G.**, Kretzberg J., Kurtz R., and Warzecha A-K.: Neuronal encoding of behaviourally relevant visual-motion information in the fly. *TINS*: **25**, 94-100, (2002).
- O13. Karmeier K., **Krapp H.G.**, and Egelhaaf M.: Robustness of the tuning of fly visual interneurons to rotatory optic flow. *Journal of Neurophysiology*, **90**: 1626-1634 (2003).
- O14. Matheson T., **Krapp H.G.**, and Rogers S.M.: Plasticity in the visual System is correlated with a change in life-style of solitarious and gregarious locusts. *Journal of Neurophysiology*, **91**: 1-12 (2004).
- O15. Franz MO, Chahl JS, and **Krapp H.G.:** Insect inspired estimation of self-motion. *Neural Computation* **16**: 2245-2260, (2004).
- O16. Gabbiani F, **Krapp H.G.**, Hatsopoulos N., Mo C-H., Koch C. and Laurent G.: Multiplication and stimulus invariance in a looming-sensitive neuron. *Journal of Physiology Paris* **98**, 19-34. (2004).
- O17. **Krapp H.G.** and Gabbiani F.: Spatial distribution of inputs and local receptive field properties of a wide-field, looming sensitive neuron. *Journal of Neurophysiology*, **93**: 2240 2253, (2005).
- O18. Karmeier K., **Krapp H.G.**, and Egelhaaf M: Population coding of self-motion: Applying Baysian inference to estimate the performance of visual interneurons in the fly. *Journal of Neurophysiology*, **94**: 2182 2194, (2005).
- O19. Gabbiani F. and **Krapp H.G.**: Spike-frequency adaptation and intrinsic response properties of an identified, looming sensitive neuron. *Journal of Neurophysiology*, **96**, 2951-2962, (2006).
- O20. Parsons M.M., **Krapp H.G.**, and Simon B. Laughlin: A motion sensitive neuron responds to signals from the two visual systems of the blowfly, the compound eyes and the ocelli. *Journal of Experimental Biology*, **209**, 4464 4474, (2006).
- O21. Peron S., **Krapp H.G.**, and Gabbiani F.: Influence of electrotonic structure and synaptic mapping on the receptive field properties of a collision detection neuron. *Journal of Neurophysiology*, **97**, 159 177, (2007).
- O22. Rogers S.M., **Krapp H.G.**, Burrows M., and Matheson T.: Compensatory plasticity at an identified pathway tunes a viso-motor pathway. *Journal of Neuroscience*, **27**, 4621 4633, (2007).
- O23. **Krapp H.G.:** Polarization vision: How insects find their way by watching the sky. *Current Biology*, **17**, R557 R560 (2007).
- O24. Taylor G.M. and **Krapp H.G.**: Sensory systems and flight stability: What do insects measure and why? *Advances in Insect Physiology*, **34**, 231 316 (2007).

- O25. **Krapp H.G.**: Estimation of self-motion for flight and gaze stabilization. *Navigation*, **55**, 147-158 (2008).
- O26. Huston S.J. and **Krapp H.G.**: Visuomotor transformation in the fly gaze stabilization system. <u>PLoS Biol.</u> **6**(7):e173 (2008).
- O27. Saleem A, **Krapp H.G.**, and Schultz S.R.: Spike-triggered independent component analysis: application to a fly motion-sensitive neuron. *Visual Neuroscience*, **8**(13):2, 1-16 (2008).

Manuscripts in preparation:

- O28. Huston S.J. and **Krapp H.G.**: Multisensory gating of fly neck motor neurons.
- O29. **Krapp H.G.**, et al.: Compound eye geometry facilitates optic flow processing in the fly.
- O30. Card G., Laughlin S.B., and **Krapp H.G.**: Does local motion adaptation affect local directional selectivity in optic flow processing interneurons of the fly?
- O31. Baden T. and **Krapp H.G.**: Velocity dependence of receptive field organization in optic flow processing interneuron.
- O32. Rogers S.M., Harston G.W.J., Kilburn-Toppin F., Matheson T., Burrows, M., **Krapp H.G**.: Spatial and temporal looming sensitivities in the receptive field of an identified visual interneuron differ in solitarious and gregarious locusts.
- O33. Longden K.D. and **Krapp H.G.**: State-dependent receptive field properies of optic flow processing interneurons.
- O34. Parsons M.M., **Krapp, H.G.**, and Laughlin S.B.: Multisensory integration in an identified population of self-motion processing interneurons.

Book Chapters:

- R1. Hengstenberg R., **Krapp H.**, and Hengstenberg B.: Visual sensation of self-motions in the blowfly *Calliphora*. *In*: C. Taddei-Ferretti (ed.) Biocybernetics of Vision: Integrative and Cognitive Processes. Singapore: World Scientific, (1998).
- R2. Dahmen H., Franz M.O., and **Krapp H.G.**: Extracting ego-motion from optic flow: limits of accuracy and neuronal filters. *In:* (J. M. Zanker and J. Zeil, eds.) Processing visual motion in the real world -- A survey of computational, neural and ecological constraints. Berlin, Heidelberg, New York: Springer Verlag, pp. 143-168, (2001).
- R3. **Krapp H.G.** and Wicklein M.: Central processing of visual information in insects. In: Basbaum A.I, Kaneko A., Shepherd G.M., and Westheimer G. (eds.) The Senses: A comprehensive reference. Vol. 1, Vision I, Masland R and Albright T.D. (eds.), San Diego, Academic Press, pp. 131-204, (2008)

Conference Proceedings:

- C1. **Krapp H.G.** Optic flow processing for motor control in flying insects. In: Proceedings of the 60th Annual Meeting of the Institute of Navigation, Dayton, Ohio, www.ion.org. (2004)
- C2. **Krapp H.G.**: Estimation and control of self-motion and gaze in flying insects. In: Proceedings of the 63th Annual Meeting of the Institute of Navigation, Cambridge, MA, www.ion.org. (2007)

Abstracts (reviewed & non-reviewed):

- A1. **Krapp H.** and Hengstenberg R.: Reliability of a fast method to determine locally the preferred direction of motion sensitive neurons. In: Rhythmogenesis in Neurons and Networks. Eds. N. Elsner, D.W. Richter, Thieme, Stuttgart 1992, 306.
- A2. **Krapp H.** and Hengstenberg R.: Representation of specific optical flow fields in lobula plate neurons of the blowfly *Calliphora*. In: Gene Brain Behaviour. Eds. N. Elsner, M. Heisenberg, Thieme, Stuttgart 1993, 357.
- A3. **Krapp H.**, Hengstenberg B., and Hengstenberg R.: Correspondence of dendritic field structure, receptive field organization, and specific flow patterns in visual interneurons of the blowfly *Calliphora*. In: Proceedings of the 22nd Göttingen Neurobiology Conference, Vol. II. Eds. N. Elsner, H. Breer, Thieme, Stuttgart 1994, 447.
- A4. **Krapp H.** and Hengstenberg R.: Comparison between optic flow fields and response fields of visual interneurons in the lobula plate of the blowfly *Calliphora*. In: Proceedings of the 23nd Göttingen Neurobiology Conference, Eds. N. Elsner, R. Menzel, Thieme, Stuttgart 1995, 404.
- A5. **Krapp H.** and Hengstenberg R.: Filter neurons for specific optic flow patterns in the fly's visual system. In: Proceedings of the 4th International Congress of Neuroethology, Eds. M. Burrows, T. Matheson, P.L. Newland and H. Schuppe, Thieme, Stuttgart 1995, 264.
- A6. Hengstenberg R. and **Krapp H.**: Distribution of roll motion sensitivity in the eyes of *Calliphora*: a comparison between neurons and behaviour. In: Proceedings of the 24th Göttingen Neurobiology Conference, Eds. N. Elsner, H.- U. Schnitzler, Thieme, Stuttgart 1996, 349.
- A7. Gabbiani F., **Krapp H.**, Koch C. and Laurent G: Biophysical implementation of a multiplication operation in an interneuron of the locust. Soc. Neurosci. Abstr. **23**: 613.17, 1997
- A8. **Krapp H.G.**, Gabbiani F., Koch, C. and Laurent G.: Neuronal Multiplication in the locust visual system. In: Proceeding of the 26th Göttingen Neurobiology Conference, Eds. N. Elsner, R. Wehner, Thieme, Stuttgart 1998, 410.
- A9. Franz M.O., Hengstenberg R. and **Krapp H.G.**: VS-neurons as matched filters for self-motion-induced optic flow fields. In: Proceeding of the 26th Göttingen Neurobiology Conference, Eds. N. Elsner, R. Wehner, Thieme, Stuttgart 1998, 419.
- A10. Gabbiani F., **Krapp H.**, Koch C. and Laurent G: Computation of object approach by two wide field motion sensitive neurons. In: Soc. Neurosci. Abstr. **24**: 613.17, 1998.
- A11. Petrowitz R., **Krapp H.G.**, Dahmen H. and Egelhaaf M.: The distribution of ommatidial axes in *Calliphora erythrocephala* varies with the direction of view. In: Proceeding of the 27th Göttingen Neurobiology Conference, Eds. N. Elsner, U. Eysel, Thieme, Stuttgart 1999, 439.
- A12. **Krapp H.G.** and Egelhaaf M.: Local preferred directions of visual wide field neurons and the compound eye geometry of the blowfly *Calliphora erythrocephala*. In: Proceeding of the 27th Göttingen Neurobiology Conference, Eds. N. Elsner, U. Eysel, Thieme, Stuttgart 1999, 440.
- A13. Karmeier K., **Krapp H.G.** and Egelhaaf M.: Does the receptive field organization of a blowfly visual interneuron depend on visual experience? In: Proceeding of the 27th Göttingen Neurobiology Conference, Eds. N. Elsner, U. Eysel, Thieme, Stuttgart 1999, 441.
- A14. **Krapp H.G.** and Gabbiani F.: Spatial integration of local motion stimuli by a wide-field looming sensitive neuron. In: Soc. Neurosci. Abstr. **26**: 66.1, 2000.

- A15. Egelhaaf M., Petrowitz R., Dahmen H. and **Krapp H.G.**: Adaptation of the compound eye geometry to optic flow processing in the blowfly *Calliphora*. In: Soc. Neurosci. Abstr. **26**: 368.11, 2000.
- A16. Gabbiani, F., **Krapp, H.G.**, Koch, C, <u>et al</u>.: Multiplicative computation by a looming-sensitive neuron, 24th Annual International Conference of the Engineering-in-Medicine-and-Biology-Society/Annual Fall Meeting of the Biomedical-Engineering-Society (EMBS 2002 BMES), pp. 1968 1969, 2002.
- A17. Matheson T., Basu Roy R., Copeland M., **Krapp H.G.** and Rogers S.M.: Plasticity in the visual system of solitarious and gregarious locusts. *Journal of Physiology* **547** P, p91PC, 2003.
- A18. Matheson T., **Krapp H.G.** and Rogers S.M.: Neuronal plasticity in the visual system of solitarious and gregarious locusts. *Comparative Biochemistry and Physiology A* **134** (3, suppl), S 73, 2003.
- A19. Matheson T., **Krapp H.G.** and Rogers S.M.: Adaptation to lifestyle in the visual system of solitarious and gregarious locusts. In: Proceedings of the 29th Göttingen Neurobiology Conference, Eds. N. Elsner, H. Zimmermann, Thieme, Stuttgart 2003, 483.
- A20. Karmeier K., **Krapp H.G.** and Egelhaaf M.: Population coding in the visual system of the blowfly: an experimental and modelling approach. In: Proceedings of the 29th Göttingen Neurobiology Conference, Eds. N. Elsner, H. Zimmermann, Thieme, Stuttgart 2003, 478.
- A21. Huston S.J. and **Krapp H.G.**: The visual receptive field of a fly neck motor neuron. In: Proceedings of the 29th Göttingen Neurobiology Conference, Eds. N. Elsner, H. Zimmermann, Thieme, Stuttgart 2003, 483.
- A22. Peron S.P., **Krapp H.G.**, Laurent G., and Gabbiani F.: Role of dendritic morphology in the processing of looming stimuli: a compartmental modelling study. Program No. 491.3. 2003 Abstract viewer/Itinerary Planner. Washington, DC: Society for Neuroscience, 2003. Online.
- A23. Card G, **Krapp H.G.**, and Laughlin SB: Motion adaptation does not affect the direction tuning of a neuron processing optic flow in the blowfly *Calliphora vicina*. In: University of Cambridge (2004) *Journal of Physiology* **555P** PC129, (2004)
- A24. Rogers SM, Harston GWJ, Kilburn-Toppin F, Matheson T, and **Krapp H.G.**: Receptive field organisation of a collision-detecting visual interneurone in solitarious and gregarious locusts. In: University of Cambridge (2004) *Journal of Physiology* **555P** PC130, (2004)
- A25. Matheson T, Rogers S, Kilburn-Toppin F, Harston G, and **Krapp H.G.**: Receptive field organization of a collision-detecting visual interneurone in solitarious and gregarious locusts. In: Proceedings of the 7th International Congress of Neuroethology, PO167, (2004)
- A26. Huston SJ and **Krapp H.G.**: Visual receptive field organization of sensory and motor neurons in the blowfly. In: Proceedings of the 7th International Congress of Neuroethology, PO168, (2004)
- A27. Gabbiani F and **Krapp H.G.**: Receptive field organization of a wide-field, looming sensitive neuron. In: Proceedings of the 7th International Congress of Neuroethology, PO182, (2004)
- A28. Gabbiani F and **Krapp H.G.**: Structure and receptive field input organization of a wide-field, looming sensitive neuron. In: Program No. 870.20. 2004 Abstract viewer/Itinerary Planner. Washington, DC: Society for Neuroscience, (2004). Online.

- A29. Karmeier K., **Krapp H.G.**, and Egelhaaf M.: Population coding of self-motion in the blowfly visual system. In: Proceedings of the 30th Goettingen Neurobiology Conference. (2005).
- A30. **Krapp H.G.** and Huston S.J.: Encoding self-motion: From visual receptive fields to motor neuron response maps. In: Proceeding of the 30th Goettingen Neurobiology Conference. (2005).
- A31. Wüstenberg D. and **Krapp H.G.**: Self-motion estimation and flight control in blowflies and locusts: a comparative study. In: Proceeding of the 31st Goettingen Neurobiology Conference (2007).
- A32. Parsons M.M., **Krapp H.G.**, and Laughlin S.B.: Multisensory integration: Rotation detection in the visual system of the fly. In: Proceeding of the 31st Goettingen Neurobiology Conference (2007).
- A33. Huston S.J. and **Krapp H.G.**: Integration of visual and haltere inputs in fly neck motor neurons. In: Proceedings of the 8th International Congress of Neuroethology, (2007)
- A34. Longden K.D. and **Krapp H.G.**: Activity modulation of optic flow processing neurons by an octopamine agonist in the blowfly. In: Proceedings of the 8th International Congress of Neuroethology, (2007)
- A35. Rogers S.M., **Krapp H.G.**, and Matheson T.: Compensatory plasticity at an identified synapse tunes a visuo-motor pathway in the locust. In: Proceedings of the 8th International Congress of Neuroethology, (2007).
- A36. Wüstenberg D. and **Krapp H.G.**: Optic flow processing interneurons in flies and locusts. In: Proceedings of the 8th International Congress of Neuroethology, (2007).
- A37. Saleem, A, **Krapp, HG**, Schultz, SR, Spike-triggered independent component analysis: A method for receptive field characterization. Society for Neuroscience, 2008, Page: 514.10.
- A38. Longden K.D. and **Krapp H.G.**: State-dependent coding properties of optic-flow processing cells in the blowfly visual system. Society for Neuroscience, 2008, Page:

Edited Books:

- 1. **Krapp H.** and Wägenbaur T. (Hrsg.). Künstliche Paradiese Virtuelle Realitäten. München: Fink, 1997.
- 2. **Krapp H.** and Wägenbaur T. (Hrsg.). Komplexität und Selbstorganisation Chaos in den Kultur- und Naturwissenschaften. München: Fink, 1997.

Textbook in preparation, due 1. July 2010 (deadline was recently extended)

Krapp H.G.: Neuroscience for Engineers, Imperial College Press